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IMPROVING RUST-RESISTANT STRAINS OF INLAND WESTERN WHITE PINE

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RESEARCH SUMMARY

Twenty-five years of research and development has succeeded in producing a new rust-resistant variety of western white pine. Nonetheless, this new variety has limited levels of resistance and no improvements in other traits. The authors describe a nursery test designed to produce a population of western white pine possessing many mechanisms of resistance, broad adaptability, and increased growth. Mechanisms of resistance (low needle spot frequency, slow canker appears, slow canker growth or tolerance) and growth rate will be selected on a family basis. Individuals exhibiting needle spot prevention, low needle spot frequency, premature needle shed, short shoot reaction, bark reactions, and accelerated growth will be selected from within these families and used to establish seed orchards. The authors propose separating the inland region into hazard zones and managing natural stands to develop resistance.

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INTRODUCTION

Development of blister rust-resistant western white pine (*Pinus monticola*) has been underway in the Inland Northwest since 1950. The first 25 years, known as the phase I program, resulted in the establishment of three seed orchards. The trees in these orchards are the results of two cycles of selection. The level of resistance, under nursery conditions, is expected to be about 60 percent (Hoff and others 1973) and field resistance will probably be as high as 80 percent (Bingham and others 1973). Selection of the phase I material was based mostly upon testing candidate trees with four tester trees. Candidates with high ability to transmit resistance were chosen (Bingham and others 1969).

During the early selection work on western white pine, a considerable knowledge was accumulated on the mechanisms of resistance and the existence of blister rust races (Bingham and others 1971). This knowledge was available early enough to enable us to do some last minute selection changes in the proportion of the types of resistance going into the phase I orchards. We had found that one mechanism of resistance (premature needle shed) was disproportionately high in a previously selected F_2 population (Hoff and others 1973). Adjustments were made and now only 30-40 percent of the resistance in the phase I seed orchards will result from this mechanism.

This knowledge also made us aware that resistance in western white pine to blister rust is due to many mechanisms of resistance. Some mechanisms are controlled by single genes, others are controlled by many genes (Bingham and others 1971; table 4). This knowledge, together with the need to provide a larger gene base to enable us to select for growth and form and to maintain adaptability to its environment, including native pests, resulted in the initiation of a new program to develop resistance in western white pine to blister rust -- phase II.

The purpose of this paper is to review resistance in western white pine to blister rust and describe a breeding program that has a high chance of stabilizing the resistance but at the same time maintaining the native adaptability of western white pine.

The breeding program includes four main elements. One element is a nursery test that will provide data on resistance and secondarily on growth since the nursery phase will keep trees until 6 years old. The 15-25 percent slowest growing families will be excluded. A second element is a field test, mainly for growth and form, but also for comparing resistance to blister rust in the nursery and field. A third element is a plan to allocate the resistant strain according to the degree of blister rust hazard. And the fourth element is to describe a method for developing resistance using natural selections.

LIFE CYCLE OF WHITE PINE BLISTER RUST

The heteroecious, full cycle white pine blister rust requires two hosts--white pines and *Ribes* spp., i.e., currants and gooseberries. Dicaryotic aeciospores are produced on pine, and infect the leaves of *Ribes* bushes. These spores have two nuclei per cell and are believed to behave genetically as 2N. The *Ribes* infection produces urediospores which aid in the spread of the fungus on the *Ribes* host. They are also dicarytic and behave genetically as 2N.

Teliospores appear on the old uredial infection usually after about 2 weeks of cool weather. The dicaryotic nuclie fuse to become 2N and upon germination meiosis occurs producing four 1N basidiospores. These spores close the cycle by infecting white pine.

Germ tubes produced by germination of the basidiospore generally enter the pine via stomata of the secondary needles. Less important infection courts are stomata of the primary leaves and stomata of succulent stem tissue.

In the secondary needles, the fungus produces a large mass of mycelium that causes the cells of the pine needle to change color and this becomes visible as a "needle spot." The fungus then grows toward the stem where it grows profusely within cortex and phloem tissue.

Often there is little or no growth impact on pine resulting from fungus growth. The damage is the result of the killing of branches or the whole tree after the fungus completely encircles the stem. Death probably results from disruption of the phloem and cortical tissues as the fungus produces the aeciospore stage.

RESISTANCE IN WESTERN WHITE PINE

Mechanisms of resistance in western white pine are most easily described if presented according to the infection and growth sequence of the fungus as it develops starting in the secondary needles.

The first mechanism is prevention of needle infection. In the past, trees with no needle spots were thrown out as escapes. But some recent data (Hoff and others in press) show that there is a continuous increase of this type from the most susceptible white pine (*Pinus ayacahuite*), with 1 percent uninfected seedlings, to the most resistant (*Pinus parviflora*), with 96 percent. In this same test, 24 percent of the *Pinus monticola* seedlings were uninfected. However, the trait appears to be a threshold character because it varies with the intensity of the inoculation. In another test (Hoff and others 1973) the F_1 seedlings were 1 percent clean and F_2's were 15 percent clean, indicating that a selection had been made for the trait.

The frequency of needle spots also varies. There is a tenfold difference between number of spots on seedlings of families with low and high numbers of spots (table 1 and Hoff and McDonald in press). The data resemble those that might be produced by a single nondominant gene. Families can be grouped into classes (low, medium, high), according to frequency of needle lesions.

Needle spots also come in a variety of colors, shapes, and sizes. We have published data and photographs of some (McDonald and Hoff 1975). So far, we have observed the following phenotypic variations in needle spots caused by the blister rust fungus:

1. Yellow needle spots of normal size; rust fungus with normal virulence.

2. Yellow needle spots of normal size; rust fungus with very high virulence (observed in Oregon, Region 6, USDA Forest Service, blister rust program).

3. Yellow needle spots, very small size.

4. Red needle spots, normal size; rust fungus with normal virulence.

5. Red needle spots, normal size; rust fungus with very high virulence (observed in Oregon, Region 6, USDA Forest Service, blister rust program).

6. Red needle spots, very small size.

7. Yellow island spots.

8. Red island spots.

Table 1.--*Average number of yellow needle spots on one lineal meter of needle tissue per seedling within full-sib crosses*

	Pollen parent				
Seed parent	58	19	17	22	$\bar{x}$
57	3	5	7	12	7
227	2	7	6	14	7
382	11	8	8	8	9
355	4	11	19	13	12
121	8	10	11	20	13
232	4	15	12	19	13
230	12	15	7	18	13
95	11	12	16	11	13
179	6	15	13	19	13
33	14	14	18	22	17
$\bar{x}$	6	11	12	16	12

Because resistance and suceptibility of seedlings and families to these various "races" affects the number of needle spots that develop on a seedling, spot tallies must include a description of the spot type.

Tentative segregation data indicate that there is a typical gene-for-gene relationship between the host and the red-normal, yellow-normal, and island-type spots. Resistance in western white pine to red appears to be controlled by a dominant gene, to yellow by a recessive gene, and for the island charactersitic by a dominant gene.

The fungus then grows down the needle and the next resistance reaction observed is the shedding of infected needles (McDonald and Hoff 1970). This reaction begins at about 9 months after inoculation and is complete at about 12 months after inoculation. Genetic control appears to be due to a recessive gene (McDonald and Hoff 1971).

A rust-resistance reaction is apparent in seedlings that keep their infected needles but never develop stem symptoms. This reaction appears to be initiated at the junction of the short shoot and needle fascicles when the fungus reaches the short shoot (Hoff and McDonald 1971). Genetic control of this reaction also appears to be by a recessive gene (McDonald and Hoff 1971).

The next rust symptom is the appearance of cankers in the stem. The rate of appearance of cankers varies with families (table 2). This trait appears to be controlled by several genes with a heritability of 46 percent.

Table 2.--*Number and percentage of blister rust cankers observed in the stems of western white pine seedlings 1 year after inoculation*

Family	Cankers following inoculation			
	1st year	2nd year	1st year/2nd year[1]	4th year[2]
	Number	*Number*	*Percent*	*Percent*
17 x 121	38	60	63	63
17 x 250	11	38	30	39
17 x 57	23	65	35	74
19 x 121	18	54	33	54
19 x 250	21	61	34	61
19 x 57	14	60	23	60
22 x 121	35	61	57	61
22 x 250	26	48	54	51
22 x 57	30	62	48	65
58 x 121	37	64	58	65
58 x 250	23	65	35	66
58 x 57	2	27	7	27

[1]Heritability (0.46) calculated from a 4 x 10 factorial including these crosses (author's unpublished data).

[2]By the 4th year after inoculation all cankers that will show up are observable.

After the fungus reaches the stem, a series of reactions can occur that--depending on individual and family--result in the death of the fungus. The effectiveness of this resistance depends on two separate reactions: (1) the ability of a seedling to initiate a necrotic response in the cortex after invasion by the rust; (2) the ability of a seedling to rapidly produce a strong wound-periderm. We observe in western white pine (unpublished information) and in Armand pine (Hoff and McDonald 1972), that only the host cells seem to be killed; the fungus, although not healthy, appears still to be alive, at least the cytoplasm and the nucleous of the fungus was not disrupted. Also, the small amount of data on Armand pine indicates that the effectiveness of the resistance varies with the phenology, i.e., the necrotic reaction is apparent when diameter growth begins and it is not operating during other periods.

The rate of growth of the fungus in the stem varies with individuals and families. In many trees, of the progeny tests set up by R. T. Bingham and A. E. Squillace in 1952 through 1955, the fungus had not girdled the stem by 1970, even though the fungus had reached the stem of the seedlings probably by the time the seedlings were 2-3 years old, i.e., 1 year after artificial inoculation (table 3).

Table 3.--*Number of trees per test, percentage dead due to blister rust, percentage resistant seedlings lifted and percentage still living with cankers in 1970 in the Elk Creek progeny test plot*

Test year	No. trees	Percent Dead rust 1970	Cankered and percent living in 1970 with old cankers[1]	with basal cankers[2]	with young cankers[3]	Percent lifted
1952	2333	78.5	1.5	0.8	1.2	18.8
1953	740	83.4	1.4	.6	1.1	14.2
1954	941	73.4	4.7	1.0	1.2	20.7
1955	1678	60.5	8.5	.8	16.4	14.5
All controls	405	94.3	0.2	.2	1.7	3.7

[1]Old cankers are cankers that resulted from infection soon after the trees were outplanted.

[2]Basal cankers appear to be cankers that resulted from the initial inoculation when the seedling was 2 years old when in the nursery.

[3]Young cankers are those that have shown up recently--3 years prior to the 1970 rust inspection.

[4]Bingham lifted these seedlings with "high" resistance and moved them to the Moscow Arboretum 1957-1960.

The last reaction type that we have observed is what is called tolerance. This is a reaction of one seedling that enables it to sustain a great amount of infection without serious growth reduction or mortality. This reaction shows up at very low frequencies.

The mechanisms of resistance are summarized in table 4, with an indicated epidemiological type and hypothetical genetic control.

Table 4.--*Observed resistance mechanisms in* Pinus monticola: Cronartium ribicola *system*

	Mechanism of resistance	Resistance type	Hypothesized inheritance	h^2
1.	Resistance in secondary needles to a yellow-spot forming race	Vertical	Recessive gene	
2.	Resistance in secondary needles to a red-spot forming race	Vertical	Dominant	
3.	Resistance in secondary needles to a yellow-green-island spot forming race	Vertical	Dominant gene ?	
4.	Resistance in secondary needles to a red-green-island spot forming race	Vertical	Dominant gene ?	
5.	Resistance in secondary needles that prevents spot formation	Vertical	?	
6.	Reduced frequency of secondary needle infections	Horizontal	Nondominant gene ?	0.37
7.	Slow fungus growth in secondary needles	Horizontal	Polygenic	.46
8.	Premature shedding infected secondary needles	Vertical	Recessive gene	
9.	Fungicidal reaction in short shoot	Vertical	Recessive gene	
10.	Fungicidal reaction in stem	Vertical	Oligogenic ?	.367
11.	Slow fungus growth in stem	Horizontal	Polygenic ?	0.21-0.46
12.	Tolerance to infection	Horizontal	?	

SELECTION OF STANDS AND PHENOTYPICALLY RESISTANT TREES

This base of knowledge has enabled us to recommend a program for the development of resistance in western white pine to blister rust that would have higher stability and genetic diversity. The methods for doing this are the topics of the remainder of this paper.

Stand Selection

There are hundreds of stands and thousands of individuals to choose from. A little time spent in the selection of "good" stands can make the program more efficient and very effective. The criteria that we feel are important in selection follows.

1. Blister rust infection is uniformly heavy, ranging upwards from a low average of 10 cankers per tree.

2. Stand age 25+ years, height 10-30 m, meaning that all trees have been exposed to natural inoculation by the rust fungus for at least 25 years, that they are climbable, and are producing cones.

3. Stand density open to moderately open, especially in older (50-to 70-year-old) stands, meaning that white pine crowns can be seen or examined with binoculars from some distance.

Selection of Individual Trees

1. Candidate trees must be relatively free from blister rust cankers under locally heavy rust conditions. Past experience has shown that under conditions of heavy infrection candidates with one or a few cankers are likely to be just as valuable as those completely free of rust. Thus flexible criteria (allowable number of cankers increasing with local rust intensity) will hold for selecting candidate trees, as follows:

Rust intensity in the stand (average number of cankers/tree)	Maximum allowable infection per candidate (number of live or dead cankers)
10-20	none
21-40	1
41-75	2
76-150	3
151+	4-5

2. Candidate trees should be close to roads so that time and effort is not wasted in their relocation (by hand compass and pacing) for examination, pollination, cone collection, or when revisited for a variety of other purposes. Generally, in denser stands where visibility is limited it is best not to locate candidates more than 100 m from the road.

3. Runty, seriously deformed (especially multi-forked), seriously diseased (other than by blister rust), or seriously insect-attacked trees should be avoided, because these poor characteristics could be inherited. This includes open-grown trees that are one-fourth or more shorter than surrounding trees of equivalent age and crown class, trees that have repeated stem forks, trees that have several whorls bearing 10 or more large branches, and trees with sinuous or crooked stems not associated with likely mechanical injuries.

INOCULATION OF SEEDLINGS WITH RUST

Bingham (1972) reviewed inoculation procedures that have been used for developing blister rust resistant western white pine at Moscow. Briefly, these procedures are as follows:

1. Inoculate seedlings after the second growth period. The typical 2-year-old seedling is about 10 cm tall, has mostly secondary needles with a few remnant primary leaves. Much of the resistance is in the secondary needles; therefore if 1-year-old seedlings were inoculated many mechanisms of resistance would be missed.

2. Use natural inoculum from several sites and thoroughly mix the infected *Ribes* leaves before placing them over the seedlings. This will assure a good mixture of rust races.

3. The *Ribes* leaves are layered on wire screening 30-40 cm above the seedlings.

4. Humidity is kept as near 100 percent as possible and the temperature between 15°-20°C. This is achieved by either enclosing the set-up with plastic that is shaded by canvas (Bingham 1972) or by layering wet burlap over wire screens (Patton and Riker 1966). Maintain test conditions for 72 hours.

In the Moscow, Idaho, environment seedlings are inoculated during the first 2 weeks of September.

RUST INSPECTION

First Rust Inspection

Timing: In Moscow, Idaho, environment, June, 9 months after inoculation.

Criteria: Count needle spots on secondary needles of each seedling by color type, on uppermost two fascicles and measure length of fascicles. This sampling method depends upon attaining at least 8 spots per lineal meter of needles. If it is much less, this sample will be inadequate and either more fascicles should be added to sample or all the spots on the tree counted. Adding more fascicles adds a lot of time and counting all spots decreases precision, so a strong effort must be given to the inoculation procedure to make sure that an adequate number of spots are produced.

Second Rust Inspection

Timing: In Moscow, Idaho environment, September, 1-year after inoculation.

Criteria: Determine the presence of needle spots on secondary needles plus stem symptoms of each seedling. Four major stem symptoms are: normal cankers; small circular, shallow necrotic areas of sunken bark associated with the base of a single needle bundle; shallow or deep necrotic areas in the needle portion of the seedling stem that partially encircle the stem; shallow or deep necrotic areas in the needle portion of the seedling stem that completely encircle the stem.

Third, Fourth, and Fifth Rust Inspections

Timing: In Moscow, Idaho, environment, September, 2, 3, and 4 years after inoculation.

Criteria: Determine the presence of stem symptoms as listed under second rust inspection plus health of each seedling.

SELECTION PHILOSOPHY AND METHODS

New varieties of western white pine resistant to blister rust must include as many of the known kinds of resistance as possible (table 4). Natural host:parasite systems evolve an optimum balance of the various mechanisms of resistance (Harlan 1976). We hope to anticipate such a balance in the proposed selection scheme, or at least come close enough so that natural adjustments could be accomplished without serious disruptions.

We have drawn freely from the literature and experience of the crop breeders to develop a selection scheme. Although there may be major differences between forest tree species and crop plants, in principles of selection they are very similar. The following principles exemplify the prevailing philosophy of the interaction host:parasite systems:

1. Resistance is the rule, susceptiblity is the exception.

2. Mechanisms of resistance vary in type and frequency.

3. Some mechanisms of resistance bestow to their carriers complete resistance, others slow the disease or curtail its development.

   a. Mechanisms that bestow complete resistance are typically controlled by single genes and are called vertical or differential resistance.

   b. Mechanisms that slow or curtail disease are typically polygenetically inherited and are called horizontal, uniform, or field resistance.

4. Vertical resistance can be neutralized by a complementary gene in the disease-causing organisms.

5. Horizontal mechanisms of resistance are not neutralized by new races; however, more aggresive races might decrease the effectiveness of the horizontal resistance.

6. Combinations of several vertical resistance genes exhibit characteristics of horizontal resistance.

7. Disease-causing organism are also restricted by their own natural fitness requirements.

8. Resistance is the observed expression of the interaction of host genes, pest genes, and environment. The level of resistance required changes with environment, weather, and disease cycle. Low levels of genetic resistance in a population often result in high levels of phenotypic expression.

9. Resistance composed of horizontal types exhibits more stability than resistance composed of vertical types.

These principals lead to the following guidelines for development of new varieties of western white pine:

1. Never base resistance on only one gene. A variety of western white pine could be produced that would be 100 percent resistant, but it probably would not last long.

2. Use combinations of resistance types--diversity is essential.

3. Incorporate as many horizontal resistance types as possible.

4. Maintain a fairly low gene frequency for all the vertical resistance types, i.e., 0.3 to 0.4 or less. Two recessive genes with a frequency of 0.5 would result in complete resistance in 42 percent of the progeny as tested in the nursery. Addition of single genes increases resistance rapidly, but since field resistance tends to be even higher than nursery resistance (Steinhoff, 1971; Bingham and others 1973), a high gene frequency of any one gene is just not needed.

SELECTION FOR RESISTANCE

Arrangement of Data and Selection Criteria

The method of rust inspection will permit the ranking of families according to: (1) fewest to highest number of needle spots--type 6, table 4; (2) slowest to fastest stem symptom appearance--type 7, table 4; (3) lowest to highest level of mortality--types 11 and 12, table 4. Individuals can be tagged for: (1) percentage of needle infections--type 5, table 4; (2) few needle spots--type 6, table 4; (3) premature shedding of infected needles--type 8, table 4; (4) the reaction type that maintains infected needles but does not develop stem symptoms (short shoot reaction)--type 9, table 4; (5) stem reaction types--type 10, table 4.

This management of data will permit the selection of the seed orchard trees as follows:

1. Individual and family selection for reduced frequency of secondary needle spots.

2. Family selection for slow fungus growth in the secondary needles.

3. Family selection for slow fungus growth or tolerance in the stem; at the seedling stage it is impossible to separate these mechanisms.

4. Individual selections for prevention of needle infections, premature shedding of infected needles, short shoot reactions, and stem reactions.

Selection Intensity

The amount of gain that will be made is directly dependent on the proportion of resistant families and individuals saved. Three major points that must be considered are first the number of families available, second the minimum number of families that will be included in a seed orchard, and third the regional planting area for each seed orchard.

So far, over 3,000 phenotypically resistant white pine have been located within the inland range of western white pine. This is just a small sample of the number available. Several more thousand could be added if necessary to increase the selection intensity.

The number of families required in a regional planting area, i.e., breeding zone or adaptive provenance, is difficult to predict. Alfalfa breeders, who are working with a species that has high genetic variations, and who have gone through several generations of breeding, suggest 75 nonrelated individuals per planting area (Hanson and others 1972). Because white pine also contains high genetic variation (Steinhoff 1979) we recommend 100 families per regional planting unit.

There is very little variation in inland western white pine that is associated with latitude, longitude, or elevation (Steinhoff 1979), meaning that there is only one regional planting unit or breeding unit. And only one seed orchard is needed for the entire inland area of white pine.

With 3,000 families to start with and with inclusions of 100 families in the seed orchard, only 1 out of 30 of the candidate trees need to be saved. One-hundred families with the highest combinations of horizontal resistance would be chosen. Individual seedlings with the various vertical resistance types will be chosen from within these families.

We recommend that the level of resistance imparted by the vertical resistance genes be in the range of 50-60 percent. This will provide trees within the population upon which the fungus can grow, but because these trees will by chance also contain genes for horizontal resistance, they will not all die. Although there is much argument in the agronomic field, it is possible that permitting the "old" races to survive will have a stabilizing effect on the rust, i.e., the rust is not apt to develop a new race to survive.

Natural Selection — An Alternative Breeding Method

There are probably at least 20-30 genes that control blister rust resistance in western white pine. There are many genes that cause the death of the fungus and there are many more genes that slow the epidemic or slow the fungus growth so that fewer trees die. With this kind of genetic variation, we could just let nature run its course. The only real drawback is nature's way takes too long. But what could be done is to manage white pine stands to speed up nature's process.

UTILIZATION OF RESISTANCE — HAZARD MAPPING

In the previous section of this paper we recommended that the production of a variety of western white pine contain moderate levels of complete resistance (50-60 percent) on a base of horizontal resistance. A variety with this level of resistance would be planted throughout the inland range of white pine. However, at this time and for a decade or two in the future, there will not be enough seed to fill the planting needs.

More seed would be available if the level of resistance was matched to the degree of hazard: the intensity of blister infection. The degree of hazard faced by white pines depends on the temperature, moisture, and wind conditions during periods of basidiospore release. The seasonal weather pattern influences the multiplications of the rust on the ribes patches as does the species of *Ribes*. The point is, that various features of weather, ribes species, and distribution and topography can be measured to produce hazard maps (McDonald and others, in press). Then seed with varying levels of resistance can be matched to each site. For example, on the highest hazard sites, seedlings with the best resistance would be planted, on less hazardous sites seed could be collected from candidate trees (level of resistance 25-

30 percent) or from the surviving trees within stands that have had high mortality due to blister rust (level of resistance 10-15 percent).

Shelterwood or seed trees of white pine that have survived the epidemic could be left to regenerate a prepared site. In many stands (60-80 years old) mortality of white pine by blister rust is 90 percent. Nonetheless, there are usually 20-30 living trees per acre that survive. When such a stand is cut or salvaged, several of these trees can be left to provide seed for regeneration. According to our data about 20 percent of the seedlings will be resistant under nursery conditions (Hoff and others 1976).

Besides regenerating a stand, this approach has other benefits. In contrast to artificial selection, nature selects for all mechanisms of resistance. Man selects for only those he can see. Also, nature uses all races of blister rust over the many inoculation years. Man uses only those he collects and usually only once for each progeny test.

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The Intermountain Station, headquartered in Ogden, Utah, is one of eight regional experiment stations charged with providing scientific knowledge to help resource managers meet human needs and protect forest and range ecosystems.

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